

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
GOEDENIA RUFIPES (CURRAN) (DIPTERA: TEPHRITIDAE) ON
ISOCOMA ACRADENIA (E. GREENE) E. GREENE IN
SOUTHERN CALIFORNIA**

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Abstract.—*Goedenia rufipes* (Curran) is an oligophagous, nonfrugivorous, fruit fly (Diptera: Tephritidae) producing at least two, probably three, annual generations altogether in the flower heads of *Chrysothamnus teretifolius* (Durand and Hilgard) H. M. Hall and *Isocoma acradenia* (E. Greene) E. Greene in southern California. Both of these confirmed hosts are Asteraceae belonging to the subtribe Solidagininae of the tribe Astereae. The egg, second- and third-instar larvae, and puparia are described and figured, and selected characteristics of these stages are compared with those of *G. timberlakei* (Blanc and Foote), the only other well-known species of *Goedenia*. The egg of *G. rufipes* is the first pictured for this genus; it bears a prominent pedicel with semicircular to fusiform micropyles. The second instar is white, but the third instar has a dark brown to black venter on the meso- and metathorax and a similarly darkened caudal segment. The prothorax and gnathocephalon of the second and third instars are smooth, mostly free of the minute acanthae that circumscribe most other body segments. Minute acanthae cover the posterior end of the truncated caudal segment, which also is perforated by scattered, open pores. The third instar lacks oral ridges. The anterior thoracic spiracle of the second instar bears three papillae, which are reduced to two papillae in the third instar. The life cycle is of the aggregative type and overwintering occurs in dead flower heads as prepupal third instars, as puparia in an open, central cells loosely surrounded by floret fragments and intact undamaged achenes, and as unmated, sexually immature adults. *Eurytoma* sp. (Hymenoptera: Eurytomidae) and *Pteromalus* sp. (Hymenoptera: Pteromalidae) are reported as solitary, larval-pupal endoparasitoids, and *Eupelmus* sp. (Hymenoptera: Eupelmidae) as possible solitary endoparasitoids.

Key Words: Insecta, *Goedenia*, *Chrysothamnus*, *Isocoma*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, aggregative life cycle, seed predation, parasitoids

Most indigenous, western North American Myopitini (Diptera: Tephritidae; Tephritinae) formerly assigned to the Palearctic genus *Urophora* Robineau-Desvoidy were reclassified in the genus *Goedenia* by Freidberg and Norrbom (1999). To date, the life history and immature

stages of only one of the eight known species of *Goedenia* have been described in detail, i.e., *G. timberlakei* (Blanc and Foote), by Goeden et al. (1995). This paper describes the life history and selected immature stages of a second species, *G. rufipes* (Curran).

MATERIALS AND METHODS

The present study utilized specimens of adults reared from 1-liter samples of mature flower heads of *Chrysothamnus teretifolius* (Durand and Hilgard) H. M. Hall and *Isocoma acradenia* (E. Greene) E. Greene (Asteraceae) collected throughout southern California since 1980 (Goeden 1987). The life history study and description of the immature stages of *G. rufipes* were based in large part on dissections of samples of mature and immature flower heads of *I. acradenia* collected east of Ocotillo at Coyote Wells and at 42-m elevation, southwestern Imperial Co., during 1990–1999. One-liter samples of excised, immature and mature flower heads containing the scarce larvae and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Ten ova dissected from a gravid female as well as two second- and 22 third-instar larvae, and nine puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, studied and digitally photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Five arenas each consisting of a clear-plastic, petri dish were provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994). Each arena contained a vir-

gin male and female obtained from emergence cages that were used for observations of courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001a, b, c), Goeden et al. (1993), Goeden and Headrick (1992), Goeden and Norrbom (2001), Goeden and Teerink (1997), Teerink and Goeden (1999), and our earlier works cited therein. Means \pm SE are used throughout this paper. Digitized photographs used to construct text figures were processed with Adobe Photoshop® Version 6.

RESULTS AND DISCUSSION

TAXONOMY

ADULT.—*Goedenia rufipes* was described from Arizona as *Aleomyia rufipes* by Curran (1932), who shortly thereafter reclassified it as *Euribia rufipes* (Curran 1934, as cited by Foote et al. 1993). Foote (1965) assigned it to *Urophora*, which Steyskal (1979) adopted in his key to Myopitinae genera and species of *Urophora*. Freidberg and Norrbom (1999) redesignated most of the indigenous, western North American species as *Goedenia*, with *A. rufipes* Curran as the type species.

The wing was figured by Curran (1934, as cited by Foote et al. 1993), Steyskal (1979), and Foote et al. (1993). Freidberg and Norrbom (1999) provided line drawings of the head in lateral and anterolateral view and the hypandrium and phallopodeme in dorsal view.

Immature stages.—The egg, second- and third-instar larvae, and puparium of *G. rufipes* are described below.

Egg: Sixteen ova dissected from a 17-day-old female were white, opaque, smooth, elongate-ellipsoidal, 0.55 ± 0.008 (range, 0.48–0.60) mm long, 0.18 ± 0.005 (range, 0.14–0.20) mm wide, smoothly rounded at tapered basal end (Fig. 1A);

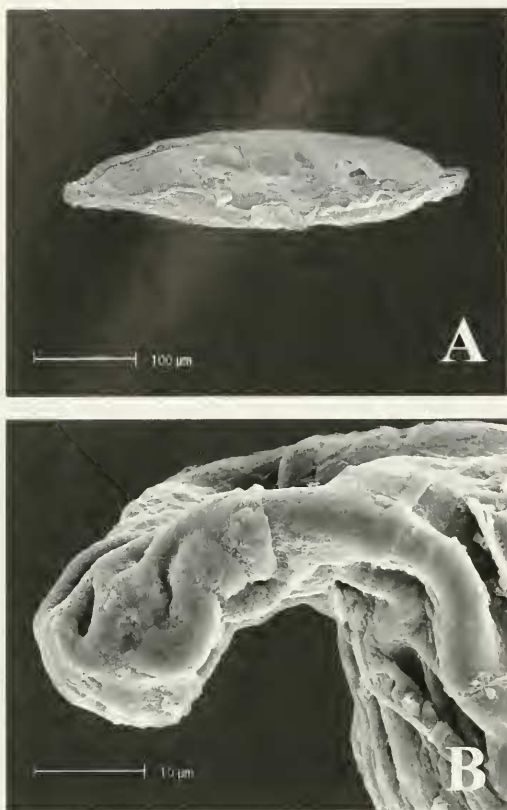


Fig. 1. Egg of *Goedenia rufipes*: (A) habitus, anterior to left; (B) pedicel showing pattern and shapes of aeropyles (probably distorted).

pedicel prominent, 0.03 mm long, circumscribed apically by different-sized, semicircular to fusiform aeropyles arranged singly or in two rows with their long axes parallel to the long axis of the egg (Fig. 1B).

The ova of *G. rufipes* on average equalled in length the ova of *G. timberlakei* and were slightly wider, but otherwise agreed with the description provided by Goeden et al. (1995). Unfortunately, the scanning electron micrograph of a possibly deformed pedicel of *G. rufipes* (Fig. 1B) is the only view of this structure obtained for this genus to date. The eggs and first instars of *Goedenia* spp. are very small, extremely difficult to find and probably are available for only a short period in nature; moreover, their study is further complicated by the tendency of these tephritids to co-occur

with other tephritid genera, i.e., *Neaspilota*, *Procecidochares*, *Trupanea*, in flower heads of the same host ("symphagy", Goeden 1997), usually in subordinate numbers, as reported by Goeden (1987).

Second instar larva: White, cylindrical, tapered anteriorly, bluntly rounded posteriorly (Fig. 2A); gnathocephalon conical (Fig. 2B), smooth, with few minute acanthae ventrally (Fig. 2B-1), lacking oral ridges (rugose pads); dorsal sensory organ well-defined, round, flattened (Figs. 2B-2, C-1); anterior sensory lobes (Figs. 2B-3, C-2), separated by vertical medial cleft, with terminal sensory organ (Figs. 2B-4, C-3), lateral sensory organ (Fig. 2C-4), supralateral sensory organ (Fig. 2C-5), and pit sensory organ (Fig. 2C-6); stomal sense organ (Figs. 2B-5, C-7) ventrolaterad of anterior sensory lobe and fused (Fig. D-1) with lateralmost of five, foliose, protrudent, lateral integumental petals (Figs. 2C-8, D-2) dorsad of each mouthhook, two vertical pairs of medial integumental petals between anterior sensory lobes (Fig. 2C-9); mouthhook (Figs. 2B-6, D-3) bidentate (Fig. 2D-3); median oral lobe laterally compressed, apically tapered (Fig. 2D-4), separated from labial lobe (Fig. 2D-5); verruciform sensilla circumscribe posterior third of gnathocephalon dorsomedially, dorsolaterally, and laterally (Fig. 2B-7); anterior spiracle with three, subglobose papillae (Fig. 2E); minute acanthae (Fig. 2F) posteriorly directed, spatulate, apically rounded on anterior fourth of meso- and metathorax venters and circumscribing all but posterior three-fourths of first abdominal segment (A1), most of A2 to A6, all but posterior three-fourths of A7, and anterior half of A8. Posterior surface of caudal segment not viewed.

The habitus of the second instar of *G. rufipes* (Fig. 2A) approximates that of *G. timberlakei* (Goeden et al. 1995). Differences noted include five lateral integumental petals in *G. rufipes* (Figs. 2C-8, D-2), not four, as pictured for *G. timberlakei* (Goeden et al. 1995). Moreover, the latter

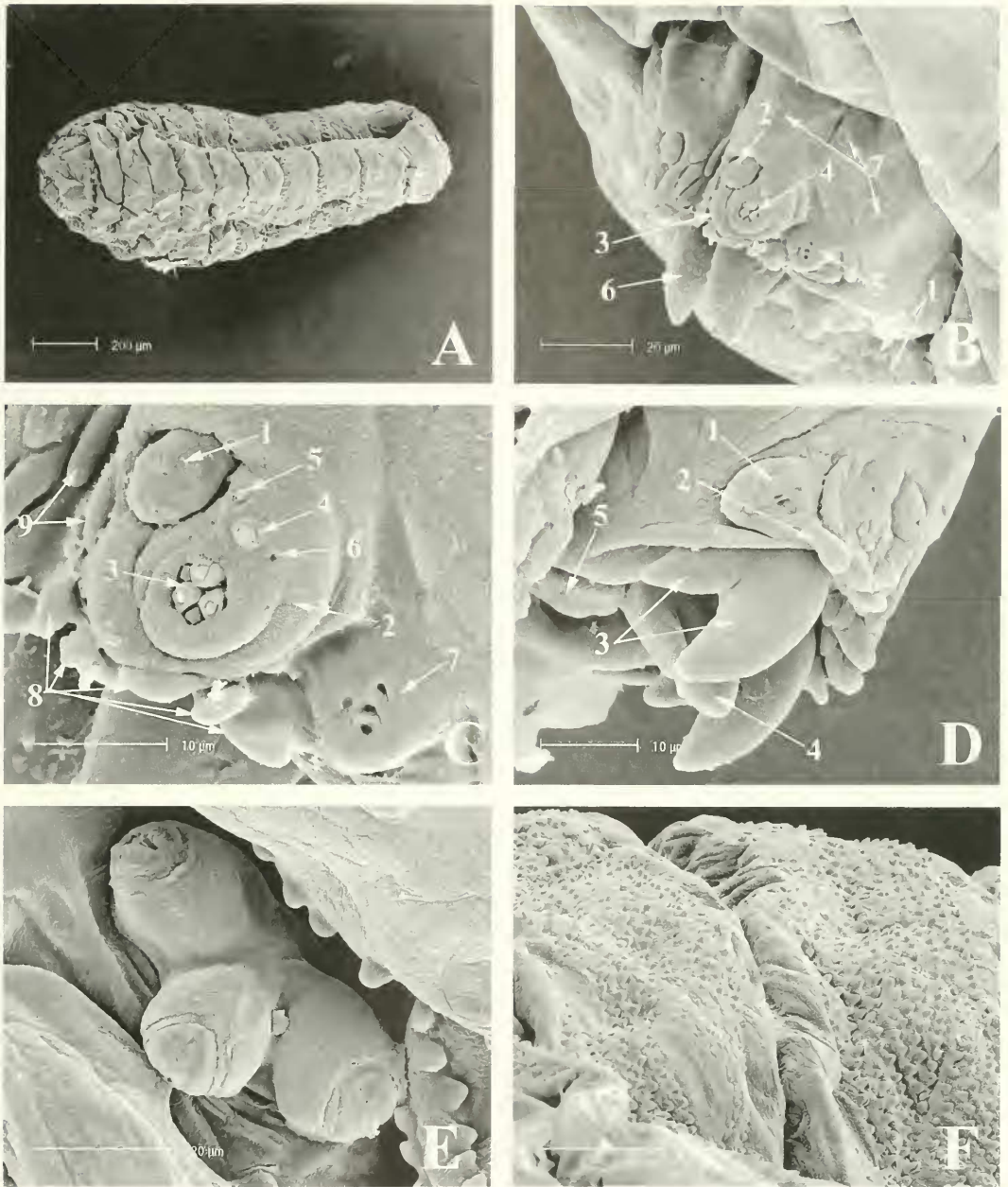


Fig. 2. Second instar of *Goedenia rufipes*: (A) habitus, anterior to right; (B) gnathocephalon, frontolateral view, 1—minute acanthae, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—terminal sensory organ, 5—stomal sense organ; 6—mouthhook, 7—verruciform sensilla; (C) gnathocephalon, close-up, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—stomal sense organ, 8—lateral integumental petals, 9—medial integumental petals, mouthhook; (D) oral cavity of gnathocephalon, ventrolateral view, 1—stomal sense organ, 2—lateralmost integumental petal, 3—mouthhook, 4—median oral lobe, 5—labial lobe; (E) anterior spiracle; (F) minute acanthae on dorsolateral aspect of abdominal segments 1 and 2, anterior to left.

species appears to have only a single pair of medial integumental petals (Goeden et al. 1995), not two pairs, like *G. rufipes* (Fig. 2C-9). The numbers of these integumental petals were not quantified by Goeden et al. (1995), but their presence and general positions were noted and pictured. Another difference is that the anterior spiracle of the second instar of *G. rufipes* bears three papillae (Fig. 2E), not two papillae, like *G. timberlakei* (Goeden et al. 1995).

Third instar larva: Oblong-ellipsoidal, roundly tapered anteriorly, bluntly truncated posteriorly (Fig. 3A), integument white, but venter of meso- and metathorax with dark brown to black infuscation (Fig. 6B); caudal segment dark brown or black (Figs. 6B, C); outwardly or posteriorly directed, conical, bluntly or sharply pointed (Figs. 3B-1, F-1) or hemispheroidal (Figs. 4C-1, E-2, F-2) minute acanthae circumscribe anterior fourth of meso- and metathorax and first abdominal segment (A1) and cover all venters thereof, and circumscribe all but anterior and posterior fifths of A2-A5, all but posterior quarter of A-7, and cover posterior plate of caudal segment (Figs. 4D-2, E-2, F-2); prothorax smooth, lacking minute acanthae (Fig. 3B), but circumscribed by verruciform sensilla dorsally, dorsolaterally, laterally, and ventrolaterally (Fig. 3B-2); gnathocephalon conical, anteriorly flattened, and medially divided by vertical cleft (Figs. 3B-3, C), pore dorsoposteriorad of each dorsal sensory organ (Fig. 3C-1); dorsal sensory organ well-defined, hemispherical (Figs. 3C-2, D-1); anterior sensory lobe (Figs. 3C-3, D) bears terminal sensory organ (Figs. 3C-4, D-2), lateral sensory organ (Fig. 3D-3), supralateral sensory organ (Fig. 3D-4), and pit sensory organ (Fig. 3D-5); two medial, papilliform integumental petals (Figs. 3C-5, D-6, E-1), four, lateral, spatulate or papilliform, integumental petals (Figs. 3C-6, D-7, E-2) above each mouthhook (Figs. 3C-7, E-3), lower, lateral petal separate from stomal sense organ (Figs. 3C-8, D-8, E-4) ventrolaterad of anterior sensory lobe; none (Figs. 3C, D), or sometimes

one, oral ridge (Fig. 3E-5) laterad of each anterior sensory lobe; mouthhook bidentate, anterior tooth, concave ventrally (Figs. 3E-6); median oral lobe laterally compressed, apically pointed (Figs. 3C-9, E-7); anterior thoracic spiracle on posterior margin of prothorax bears two subglobose papillae (Figs. 3B-4, F-2); mesothoracic, lateral spiracular complex with six verruciform sensilla in vertical series (Fig. 4A-1), mesothoracic spiracle not seen; metathoracic lateral spiracular complex with nearly closed, lateral spiracle (Fig. 4B-1) and four verruciform sensilla (Figs. 4A-2, B-2) in vertical series posterior to spiracle; lateral spiracular complex of first abdominal segment consists of nearly closed spiracle (Figs. 4A-3, C-1) and three verruciform sensilla in vertical series posterior to spiracle (Figs. 4A-4, C-2); caudal segment with pair of posterior spiracular plates (Figs. 4D-1, E-1, F) surrounded by hemispherical minute acanthae (Figs. 4D-2, E-2, F-1) interspersed dorsomedially, medially, and less so, ventromedially with open pores (Figs. 4D-3, E-3); each posterior spiracular plate bears three, smoothly flattened, ovoid rimae (Fig. 4F-2), ca. 0.01 mm in length, and four spinose interspiracular processes, each ca. 0.004 mm long (Fig. 4F-3).

The habitus of the third instar of *G. rufipes* resembles that of *G. timberlakei* (Goeden et al. 1995). In both species, the venter of the thorax and the caudal segment are darkly pigmented (Figs. 6C, Goeden et al. 1995) and minute acanthae circumscribe the meso- and metathorax and abdomen, and especially noteworthy, the posterior surface of the caudal segment, also is dotted prominently with scattered pores (Figs. 4D-3, E-3; Goeden et al. 1995). The prothorax and gnathocephalon of both species are smooth and free of minute acanthae (Fig. 3C, Goeden et al. 1995).

Two medial and four lateral integumental petals are present in *G. rufipes* (Figs. 3C-5, -6, D-6, -7, E-1, -2); whereas, *G. timberlakei* has two medial and six lateral integumental petals (Goeden et al. 1995, un-

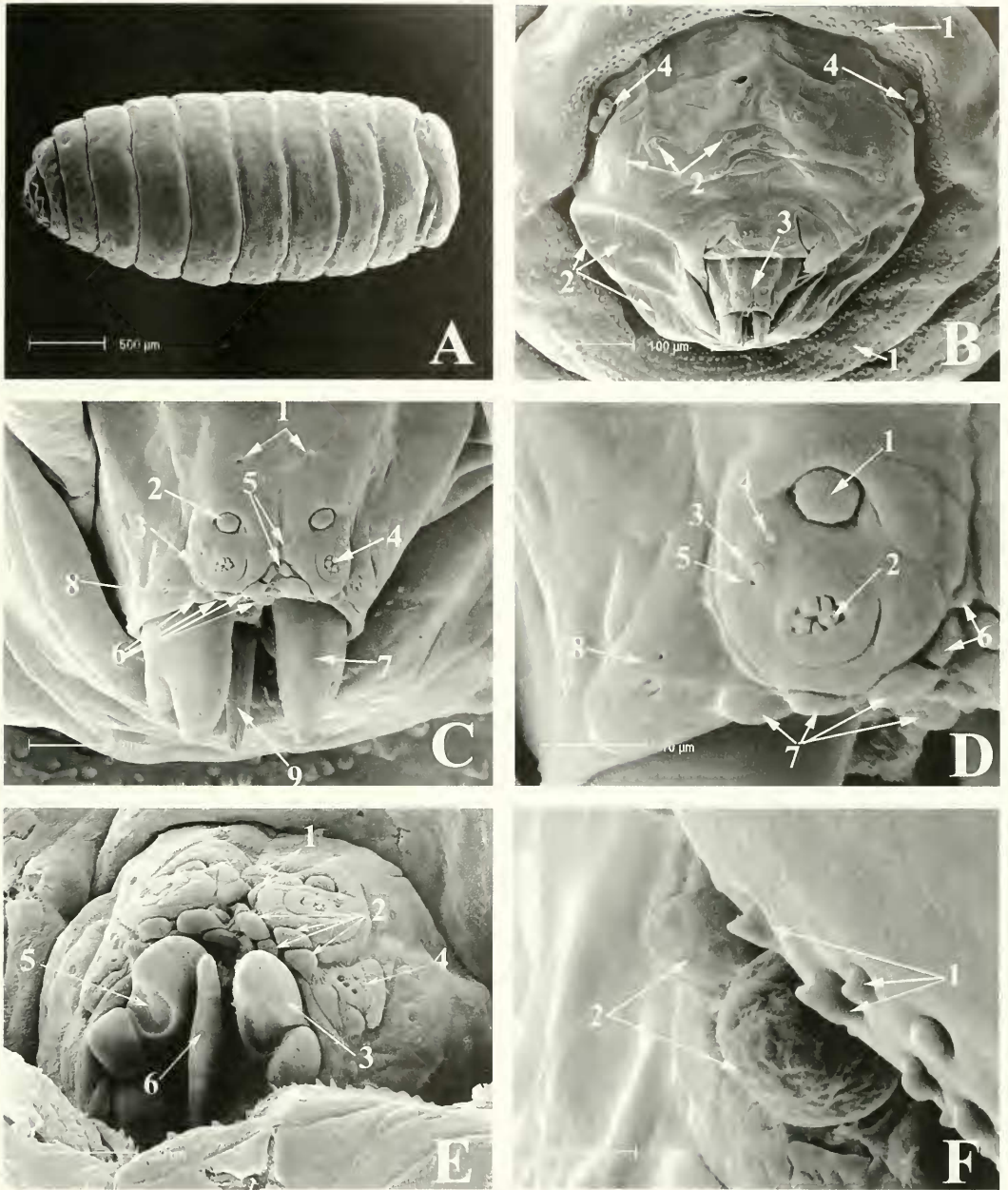


Fig. 3. Third instar of *Goedenia rufipes*: (A) habitus, anterior to left; (B) gnthocephalon and prothorax, frontolateral view, 1—minute acanthae, 2—verruciform sensilla, 3—gnthocephalon, 4—anterior spiracle; (C) gnthocephalon, frontal view, 1—pores, 2—dorsal sensory organ, 3—anterior sensory lobe, 4—terminal sensory organ, 5—medial integumental petals, 6—lateral integumental petals, 7—mouthhook, 8—stomal sense organ, 9—median oral lobe; (D) gnthocephalon, close-up, 1—dorsal sensory organ, 2—terminal sensory organ, 3—lateral sensory organ, 4—supralateral sensory organ, 5—pit sensory organ, 6—medial integumental petals, 7—lateral integumental petals, 8—stomal sense organ; (E) oral cavity of gnthocephalon, ventral view 1—medial integumental petals, 2—lateral integumental petals, 3—mouthhook, 4—stomal sense organ, 5—posterior concavity on anterior tooth of mouthhook, 6—median oral lobe; (F) anterior spiracle, 1—minute acanthae, 2—papillae.

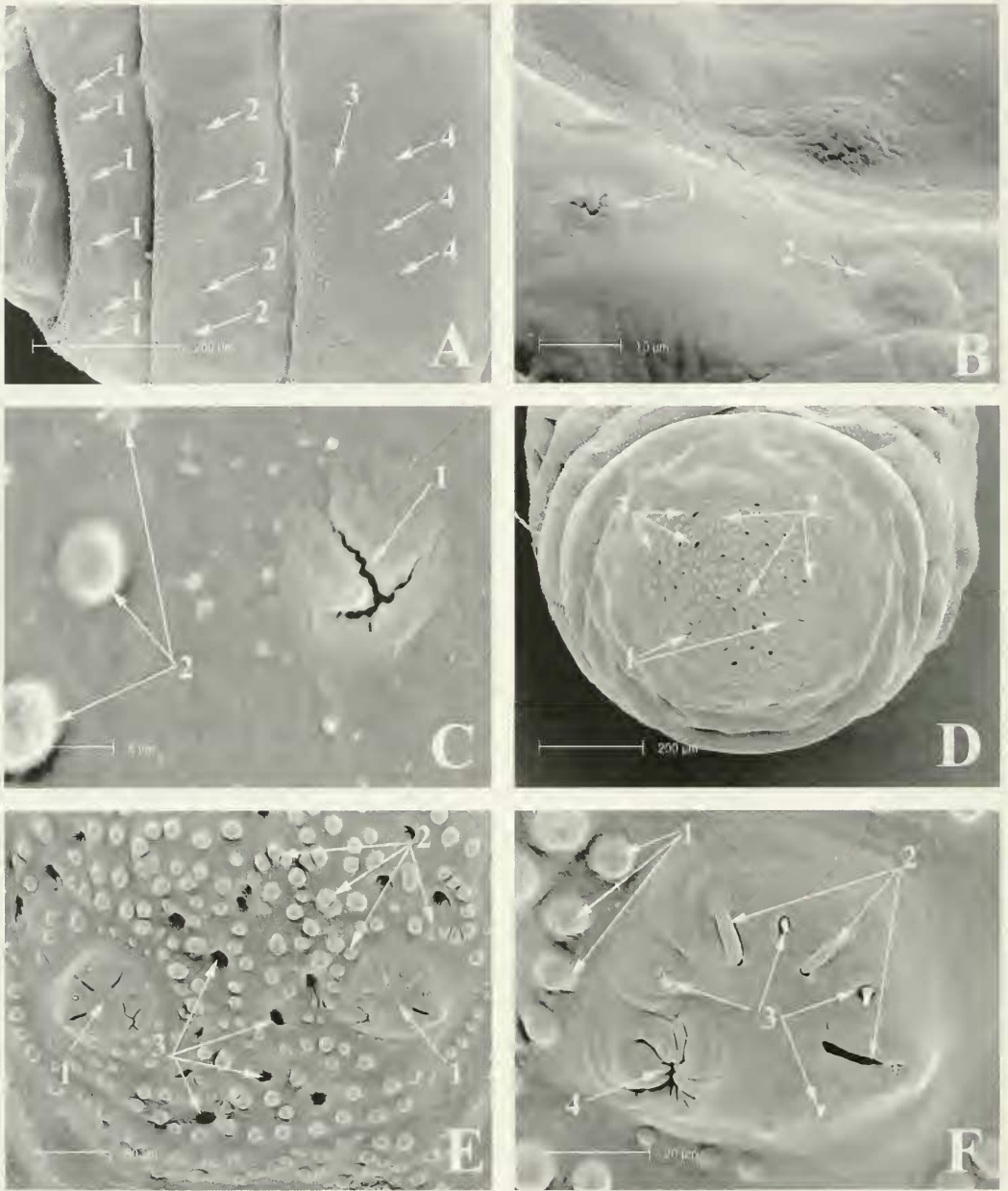


Fig. 4. Third instar of *Goedenia rufipes*, continued, (A) lateral spiracular complexes, 1—verruciform sensilla on mesothorax, 2—verruciform sensilla on metathorax, 3—spiracle on first abdominal segment, 4—verruciform sensilla on first abdominal segment, (B) 1—metathoracic lateral spiracle, 2—verruciform sensillum; (C) 1—lateral spiracle of first abdominal segment, 2—minute acanthae; (D) caudal segment, 1—posterior spiracular plates, 2—minute acanthae, 3—pores; (E) caudal segment, close-up, 1—posterior spiracular plates, 2—minute acanthae, 3—pores; (F) posterior spiracular plate, 1—minute acanthae, 2—rimae, 3—interspiracular processes, 4—ecdysial scar.

published data). The lateralmost integumental petals are separated from the stomal sense organs in both species (Figs. 3C-8, D-8, E-4; Goeden et al. 1995).

Like *G. timberlakei* (Goeden et al. 1995, unpublished data), the third instar of *G. rufipes* lacks oral ridges on either side of the mouth opening, and ventral or ventrolateral to the stomal sense organ (Fig. 3E).

The mouthhooks of the third instars of *G. rufipes* (Fig. 3E-6), like those of *G. timberlakei* (Goeden 2001c), are bidentate; however, the teeth of the latter species were described as "conical", but in the former species the anterior tooth is concave ventrally (Fig. 3E-6). Unfortunately, a vertical view of the oral cavity such as obtained for *G. rufipes* (Fig. 3E), was not obtained for *G. timberlakei* (Goeden et al. 1995, unpublished data).

The anterior spiracle of both species bears only two papillae (Figs. 3B-4, F; Goeden et al. 1995).

The lateral spiracular complex of the mesothorax of *G. rufipes* includes six verruciform sensilla in a vertical series (Fig. 4A-1); whereas, in *G. timberlakei*, this same complex includes only two verruciform sensilla (Goeden et al. 1995). Likewise, the metathoracic lateral spiracular complex of *G. rufipes* includes four verruciform sensilla (Fig. 4A-2), but again, only two such sensilla in *G. timberlakei* (Goeden et al. 1995). Finally, three verruciform sensilla in a vertical series comprise the lateral spiracular complex of the first abdominal segment of *G. rufipes* (Figs. 4A-4, C-2), but only one verruciform sensillum is found on this segment in *G. timberlakei* (Goeden et al. 1995).

Differences noted between the second and third instars of *G. rufipes* include the reduction in the number of papillae on the anterior thoracic spiracle from three (Fig. 2E) to two (Figs. 3B-4, F-2). The number of lateral integumental petals also is reduced from five in the second instar (Figs. 2C-8, D-2) to four in the third instar (Figs. 3C-6, D-7, E-2). The stability of these num-

bers is questionable, and their separation as medial versus lateral integumental petals is problematic because more precise counts and assessments would require considerably more replication of similar views of gnathocephala than were available to the author.

Puparia: Light (Fig. 6D) to dark (Fig. 6E), reddish brown with dark brown to black, anterior stripe on venter of meso- and metathorax and similarly dark caudal segment, elongate-ellipsoidal, with smoothly rounded anterior end and truncated posterior end (Fig. 5A). Anterior end bears invagination scar and raised, bilobed, anterior thoracic spiracles (not shown). Flattened posterior end of caudal segment studded with smoothly rounded, hemispherical, minute acanthae (Fig. 5B-1) interspersed with open pores (Fig. 5B-2). A pair of raised, oval, posterior spiracular plates (Fig. 5B-3) each bear three oval rimae interspersed with four, peg-like interspiracular processes (not shown, see Fig. 4F and above description of third instar for details). Ten puparia dissected from flower heads of *Isocoma acradenia* averaged 2.73 ± 0.07 (range, 2.50–3.17) mm in length; 1.15 ± 0.04 (range, 1.05–1.31) mm in width.

DISTRIBUTION AND HOSTS

To date, *Goedenia rufipes* only is known from southern California and southwestern Arizona north of Mexico (Foote et al. 1993); however, it probably ranges well into Mexico attacking flower heads at least of *Chrysothamnus teretifolius* and *Isocoma acradenia*. The former host is newly reported (Goeden 1987, Foote et al. 1993). Both of these confirmed hosts are Asteraceae belonging to the subtribe Solidaginiinae of the tribe Astereae (Bremer 1994). Accordingly, *G. rufipes* probably is a narrowly oligophagous tephritid, that to date has not been reared by me from flower heads of several other species of these two, common and widespread, plant genera. *Chrysothamnus teretifolius* occurs on rocky slopes and flats from 600 to 4,000 m in Cal-

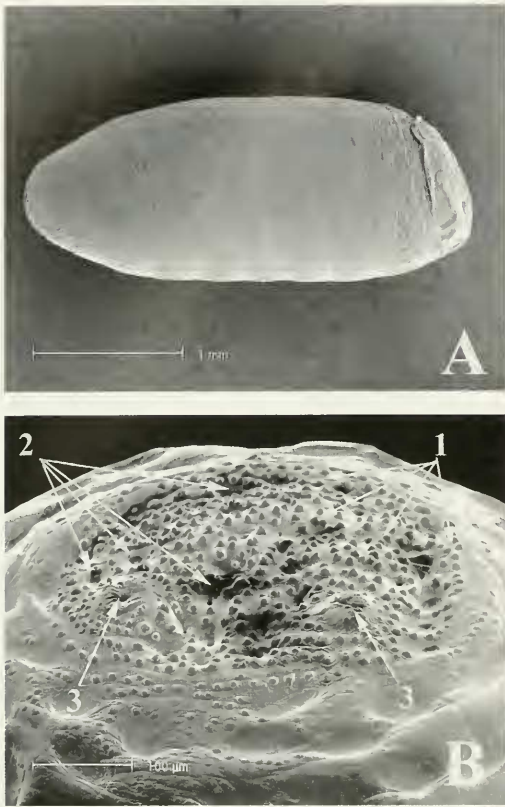


Fig. 5. Puparium of *Goedenia rufipes*: (A) habitus, anterior to left, (B) caudal segment, 1—minute acanthae, 2—pores, 3—posterior spiracular plates.

ifornia to southern Nevada and northwestern Arizona (Hickman 1993), including the higher parts of the Lower Sonoran Zone and arid, lower margins of the Upper Sonoran Zone as delimited by Shreve and Wiggins (1964). *Isocoma acradenia* occurs on sandy or clay soils in alkaline or gypsum flats or slopes below 1,300 m in California, Arizona, Nevada, and Baja California, Mexico (Hickman 1993).

BIOLOGY

Egg.—Eggs of *G. rufipes* are inserted singly, pedicel-last, parallel to the long axes of and between the outer phyllaries of closed, preblossom flower heads of *I. acradenia*.

Larva.—Upon eclosion, the first instar tunneled immediately through the inner

bracts and into an ovule of a preblossom flower head. It fed with its body perpendicular to and its mouthparts toward the receptacle within an ovule, which it first excavated, then exited and entered an adjacent ovule. The receptacle was neither abraded or pitted by such feeding.

Second instars (Fig. 6A) mainly continued feeding on ovules in closed, preblossom flower heads, but a few were found feeding on soft achenes in open, blossom or postblossom flower heads (Fig. 6A). They usually fed within the ovules or achenes with their bodies perpendicular to the receptacles, but always above the receptacles. Receptacles of 10 flower heads containing second instars averaged 1.45 ± 0.12 (range, 0.85–1.99) mm in diameter. These 10 flower heads each contained a single larva that had damaged an average of 3.2 ± 0.6 (range, 1–6) ovules/achenes, or about 28% of the average total of 11.6 ± 0.8 (range, 7–14) ovules/achenes per flower head counted within the 10 flower heads. However, more than 600 uninfested flower heads were individually dissected in order to locate these 10 (1.7%) flower heads infested with second instars.

Third instars in flower heads fed with their long axes oriented perpendicular to the receptacles, and with their mouthparts directed towards the receptacles, that they usually scored or pitted deeply (Fig. 6B, C). Fifty flower heads (three, closed preblossom; six, open blossom; 41 postblossom) were dissected that contained an average of 1.3 ± 0.1 (range, 1–4) third instars. These 55 flower heads averaged 1.8 ± 0.05 (range, 1.1–2.9) mm in diameter and contained an average total of 13.9 ± 0.4 (range, 8–20) ovules/achenes, of which on average 7.1 ± 0.5 (range, 1–15) ovules/achenes were damaged or ~51%. However, well over 1,000 flower heads were individually dissected to locate these 55 infested flower heads. Receptacles that consistently were pitted suggested that sap constituted at least part of the diet of third instars of *G. rufipes*. Goeden (1988), Headrick and Goeden

(1990), Goeden and Headrick (1992), Goeden et al. (1993, 1995), Headrick et al. (1996), Goeden and Teerink (1997) first noted, described, and discussed sap feeding by florivorous species of Tephritidae in the genera *Trupanea*, *Paracantha*, *Neaspilota*, *Tephritis*, *Goedenia* (as *Urophora*), *Dioxy-na*, and *Xenochaeta*, respectively. Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and formed puparia (Figs. 6D, E).

Pupa.—The receptacles of nine flower heads that contained an average of 1.3 ± 0.2 (range, 1–2) puparia (Figs. 6D, E) averaged 1.9 ± 0.1 (range, 1.4–2.3) mm in diameter. The receptacles were deeply pitted in all nine flower heads, further confirming that sap constituted part of the diet of third instars. The posterior end of the puparium rested in the smooth cup-like depression and the middle and anterior part of the puparium was surrounded by excavated floret fragments that formed a close, central cell not glued to the puparium.

Adult.—The premating and mating behaviors of *G. rufipes* were not studied in the field, but were observed in petri dish arenas of the type found to be useful with many other nonfrugivorous, tephritid species (Headrick and Goeden 1994). The wings of both sexes were held away from the body at about 45° without supination when at rest (Fig. 6F). Both sexes exhibited wing hama-tion (Headrick and Goeden 1994) throughout the day concurrent with other behaviors, i.e., grooming, resting, and feeding; this also was the most common wing movement reported for *G. timberlakei* (Goeden et al. 1995). Premating behaviors observed with *G. rufipes* included males and females tracking individuals of the opposite sex, during which males sometimes swayed and usually exhibited abdominal pleural distension (Fig. 6F). The male aggressively mounted a female by jumping upon her, usually from the front, then turning and forcefully grasping her wing bases, thoracic pleura, and aculeus for purchase,

while the female usually struggled, resisted his attempts to part her wings, and pushed against the male with her hind legs and tarsi. The males countered by grasping and raising the oviscapae with the mid- and hind tarsi, while positioning the apex of the exerted aculeus of a receptive female against his epandrium. Nonreceptive females did not exert their aculeus or pressed the exerted aculeus against the substrate so as to hinder or prevent proper positioning by males. But if receptive, the female allowed the male to raise her oviscapae and extended her aculeus to its full length in response to his copulatory induction behavior ("CIB"; Headrick and Goeden 1994, 1999). The CIB mainly consisted of the male rapidly rubbing his hind tarsi, back and forth, along her oviscapae. The final mating position commonly had the wings of the male parted at about 20° (Fig. 6H), the wings of the female parted at 60° (Figs. 6G, H), with both pairs of wings centered over the midlines of the flies (Figs. 6G, H). The foretarsi of the male grasped the dorsum of the abdomen of the female laterally at the thoracic juncture, the midtarsi grasped the oviscapae at its base, and the hindtarsi crossed under the oviscapae or occasionally rested on the substrate (Fig. 6I). The body of the female paralleled the substrate with the oviscapae raised about 30° , while the extended aculeus pushed the male upward and backward (Fig. 6I). Five pairs were observed to mate once or twice per day for a total of nine matings that lasted an average of 96 (range, 20–285) min. Females became restless before termination of mating by pushing against the males with their hind tarsi, by lofting their wings so as to push them against the males, and by fully extending their aculeus. The male in turn countered this behavior with CIB, rocked from side to side to regain purchase or to avoid the female's pummeling, and sometimes rapidly vibrated his wings, all of which appeared to calm the female and allow coitus to continue. Females sometimes walked about the arenas carrying the males while remaining

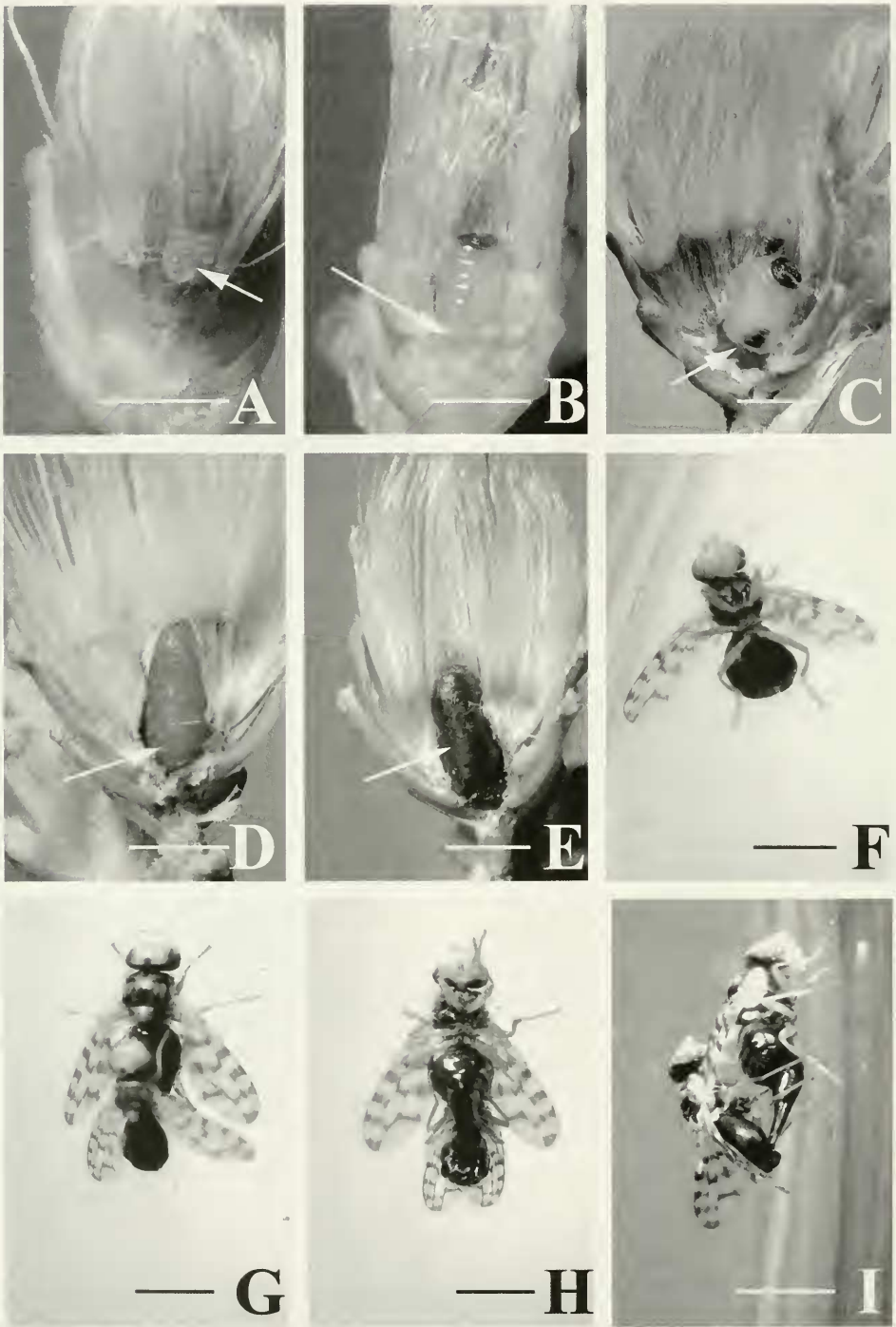


Fig. 6. Life stages of *Goedenia rufipes* (A-E in flower heads of *Isocoma acradenia*): (A) second instar (arrow) feeding on floret; (B) third instar (arrow) feeding deeply in receptacle of flower head; (C) third instar showing dark, ventral infuscation (arrow); (D) newly formed, light brown puparium (arrow); (E) dark overwintered puparium (arrow); (F) ventral view of adult male with wings in resting position with inflated abdominal pleura; (G) mating pair, dorsal view; (H) mating pair, ventral view; (I) mating pair, lateral view. Lines = 1 mm.

in copula. One male was observed to attempt mating with a newly dead female continuously for 5 h. Separations of three other pairs were observed, during which the male initially moved slightly forward while pulling the aculeus vertically upward, then rapidly turned and laterally walked off the female, and quickly posteriorly away from the female, while pulling free his genitalia. The separation of one pair took 15 s.

Seasonal history.—The life cycle of *G. rufipes* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the third instar, puparium, and some adults variously are the overwintering stages. Adults emerge from some of the puparia formed in late-fall, early winter (October–December) and these unmated, sexually immature adults overwinter. The remaining, nonfeeding third instars, prepuparia, and puparia overwinter in dead flower heads remaining on dormant *Chrysothamnus teretifolius* and *Isocoma acradenia*. These overwintered individuals emerge as adults in late winter (February–March) and either aggregate on one or more, as-yet-unknown, spring blooming, alternate hosts to mate and produce an as-yet-undetected spring generation. Or, the overwintered and newly emerged adults continue to pass the following spring and summer (April–August), possibly still as non-reproductive individuals feeding in mountain meadows and riparian habitats bordering the low-elevation, Sonoran Desert. They eventually aggregate on preblossom, fall-blooming, *C. teretifolius* and *I. acradenia*, mate, and subsequently oviposit in the small, newly-formed, closed, preblossom flower heads.

Natural enemies.—Fourteen *Eurytoma* sp. (Hymenoptera: Eurytomidae) and 12 *Pteromalus* sp. (Hymenoptera: Pteromalidae) were reared from separate puparia of *G. rufipes* as solitary, larval-pupal endoparasitoids. Two *Eupelmus* sp. (Hymenoptera: Eupelmidae) also were reared from insectary cagings of mature flower heads as possible solitary endoparasitoids, as reported

from *G. timberlakei* by Goeden et al. (1995).

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